Psychophysical investigation of vigilance decrement in jumping spiders: Overstimulation or understimulation?

Short title: Vigilance decrement in jumping spiders

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Abstract

The inability to maintain signal detection performance with time on task, or vigilance decrement, is widely studied in people because of its profound implications on attentionally-demanding tasks over sustained periods of time (e.g., air-traffic control). According to the resource depletion (overload) theory, a faster decrement is expected in tasks that are cognitively demanding or overstimulating, while the underload theory predicts steeper decrements in tasks that provide too little cognitive load, or understimulation. Using *Trite planiceps*, a jumping spider which is an active visual hunter, we investigated vigilance decrement to repetitive visual stimuli. Spiders were tethered in front of two stimulus presentation monitors and were given a polystyrene ball to hold. Movement of this ball indicates an attempt to turn towards a visual stimulus presented to a pair of laterally-facing (anterior-lateral) eyes for closer investigation with high-acuity forward-facing (anterior-median) eyes. Vigilance decrement is easily measured, as moving visual stimuli trigger clear optokinetic responses. We manipulated task difficulty by varying the contrast of the stimulus and the degree of 'noise' displayed on the screen over which the stimulus moved, thus affecting the signal:noise ratio. Additionally, we manipulated motivation by paired testing of hungry and sated spiders. All factors affected the vigilance decrement, but the key variable affecting decrement was stimulus contrast. Spiders exhibited a steeper decrement in the harder tasks, aligning with the resource depletion theory.

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Keywords: Habituation; Salience; Salticidae; Sustained attention; Selective attention; Vigilance

Introduction

Vigilance, the action or state of monitoring the surroundings for potential threats, mates or prey (Beauchamp 2015), can be defined as the probability that an animal will detect a given stimulus at a given time (Dimond and Lazarus 1974; Beauchamp and Ruxton 2012). Vigilance, however, is affected by stimulus salience, as an animal's attention may never be driven to a stimulus that is not salient, while a salient stimulus will likely attract attention (Itti and Koch 2001). Studies in animals as varied as praying mantises (Prete 1992) and humans (Helton and Warm 2008) show that detection probability reduces for low-salience signals and increases for high-salience signals. Salience may also affect sustained attention (Dukas and Clark 1995): for repetitive stimuli, the decline in probablity of response is steeper for low-salience signals compared with high-salience signals. The phenomenon of a behavioural decrement in response to repetitive visual stimuli is known as vigilance decrement (Helton and Warm 2008).

There are two competing theories of the vigilance decrement, a phenomenon which has primarily been investigated in humans: the resource depletion theory (Helton and Warm 2008) and the underload theory (Pattyn et al. 2008). Under resource depletion theory, a faster decrement is expected in tasks that are cognitively demanding (e.g., low salience, high noise), based on the assumption that the psychophysical contrast is so challenging that it 'burns up' replenishable cognitive resources necessary for attention such that the task is overstimulating (e.g., overworked neurons Helton et al. 2002), or simply that resources are reallocated. In contrast, the underload theory predicts a faster response decrement in tasks that are less challenging. This posits that an easy stimulus provides too little cognitive load, so the attentional system reduces effort through understimulation (Pattyn et al. 2008). Evidence in humans supports both theories, but this framework has not previously been applied to invertebrates.

Jumping spiders (Salticidae) are comparatively small spiders (2-10 mm as adults), with short legs and a broad cephalothorax that bears four pairs of eyes which combined have fields of view extending almost 360 degrees (Land 1985). Salticids are persistent hunters and are very attentive to moving stimuli. The forward-facing pair of principal eyes (anterior median, AM) have narrow fields of view, but combine excellent spatial resolution with colour vision. Three pairs of secondary eyes around the cephalothorax provide wide fields of view and function primarily as motion detectors (Duelli 1978; Zurek and Nelson 2012a). Of these, the anterior lateral (AL) eyes are the largest and are also forward-facing. Motion detected by the secondary eyes may elicit an orienting or optomotor response, whereby the salticid rapidly turns to face the object to examine

it using the high-acuity principal eyes. After turning to face an object, they will move closer if interested, and in the case of potential prey, slowly stalk it and ultimately pounce (Foelix 2011).

Salticids display some of the richest behaviours among arachnids (Wilcox et al. 1996; Harland and Jackson 2004; Jackson and Harland 2009; Herberstein 2011) despite having roughly 500,000 neurons (Mike Land, pers. comm.). As hunters, salticids must selectively attend to a wide range of visual stimuli. Searching for prey requires complex pattern recognition, which is a computationally demanding task (Dukas 2002), and thus animals must restrict the amount of visual information that is processed at any given time (Broadbent 1965; Milinski 1990; Dukas 1998; Kastner and Ungerleider 2000). Selective attention allows animals to respond to competing stimuli, enabling some stimuli to evoke a behavioural response while others are ignored (Blake and Logothetis 2002; Bichot et al. 2005; Paulk et al. 2014). This trait may be even more important for small-brained animals, which might otherwise face severe trade-offs (Corbet 1999; Sztarker and Tomsic 2011; Paulk et al. 2014).

Trite planiceps, the salticid species used in this study, decreases its response to repetitive visual stimuli over time (Melrose et al. In Press). It was initially suggested that this response decrement was due to habituation, a behavioural decrement in response to repeated visual stimuli caused by a decrease in neural response within the peripheral nervous system (Mackworth, 1968; Rankin et al., 2009), but conclusions about the cause of the decrement could not be made on those data alone (Melrose et al. In Press). Based on the different predictions from underload theory and from resource depletion theory, here we investigate the effect of task difficulty on the vigilance decrement to repetitive visual stimuli in *T. planiceps*. We manipulated difficulty by varying the contrast of the stimulus and the degree of 'noise' displayed on the screen over which the stimulus moved, thus affecting the signal:noise ratio. Additionally, we manipulated motivation by paired testing of hungry and sated spiders. Easy (e.g., high contrast stimulus with low noise) and difficult tasks (e.g., low contrast stimulus with high noise) were compared to explore the basis of the vigilance decrement. We predicted that if *T. planiceps* demonstrated a vigilance decrement due to understimulation, spiders would show a steeper decrement in the easy tasks relative to difficult tasks, with the converse being true if the observed decrement was due to overstimulation, or resource depletion.

Methods

Housing and Maintenance

Laboratory lighting was on a 12:12 L:D cycle commencing at 8 am. Temperature was kept constant at 25˚C. *Trite planiceps* spiders were wild-caught from rolled up flax leaves (*Phormium tenax*) in Spencer Park, in Christchurch, New Zealand. Spiders were brought to the laboratory and were fed and given a 7-day acclimation period before testing. Spiders were housed in upside down transparent plastic jars (ca. 17 x 8 cm) with a cotton roll inserted in a drilled hole in the bottom of the lid. The cotton was partially submerged in a cup of water to provide humidity. Additional holes were drilled into the opposite end of the jar; one, for ventilation, was covered with mesh and another was plugged with a cork for weekly feeding of 2-3 houseflies (*Musca domestica*). Inside the jar was a folded piece of card within which the salticids could hide and build nests.

Stimulus creation

The apparatus consisted of a holding stand, a Logitech® webcam, and two identical monitors (17'' Phillips Brilliance 170P 1280 x 1042, 75 Hz refresh rate) placed at a 120^{o} angle from each other. The monitors were standardised for brightness and colour using Spyder 4 Pro® colorimeter and software.

Stimuli crossed on the horizon of the spider's field of view and moved from posterior to anterior. Stimulus presentation was separated by a 10 s inter-stimulus interval (ISI) and was presented 80 times for each individual. The 40-pixel diameter stimuli were grey circles subtending 1.3^{o} from the point of view of the test subject and were presented amongst a cluttered background.

Stimuli (see Supp. Fig. 1) were created in Adobe Premiere CC® 2015. Firstly, a full stop was enlarged to 40 pixels and opacity was set at 10% (RGB 239, 239, 239) (group 1) or 30% (RGB 213, 213, 213) (group 2). Each stimulus presentation video was made as follows: Premiere® was configured to display media at the screen size of the apparatus (i.e., 2560 x 1042 pixels, the combined size of the two monitors). Two motion files were generated, one for each screen. The stimulus moved on screen from 13 to 8 cm, from the centre point of the screen toward the intersection of the two screens so as to coincide with the field of view of the AL eyes in this species (Melrose et al. In Press). Upon reaching the 8-cm mark, the stimulus was set to change to 0% opacity (thus disappearing) but continued moving for 10 s to create the ISI, generating a 15 s video with the circle moving for 5 s.

Task difficulty was manipulated by presenting each stimulus amongst two backgrounds of different levels of clutter, which were created separately. Clutter was generated using Adobe Photoshop® CS6 and later exported in to Adobe Premiere® CS6 Motion Effects to generate unique

movie files combining each level of clutter and either high (30%) or low (10%) contrast stimuli. Clutter was added as a foreground image with the moving stimulus set as the background layer. The output was set to 2560 x 1042 pixels and had a grey (RBG 250, 250, 250) background. To create clutter, the noise filter in Photoshop® was used to assign random pixels to the image, which allowed for manipulation of the amount of noise, type of distribution, and colour mode. A Gaussian distribution and monochromatic colour mode was used for both clutter levels, which were 20% for the low level and 40% for high clutter level.

Luminance, brightness and RGB values for each clutter level were measured within Photoshop® by averaging the whole image (Table 1). The monitors were standardized by setting the same viewing characteristics of the computer screen used for presentation to the screen used to create stimuli (100% brightness, 50% contrast and 6500K colour). Each stimulus was randomly presented on either the left or right screen, as preliminary work has established that there is no bias for left or right screens. Videos were exported as 21 min clips (80 trials) using an HEVC (H.265) codec and were presented to spiders using VLC media player 2.2.2.

Testing protocol

Nineteen female *T. planiceps* adults and sub adults were tested. Spiders were randomly split into two groups of ten and nine. One group was shown the high contrast stimulus, and the other was shown the low contrast stimulus amongst both low and high levels of clutter. Testing was carried out between 0700 to 1300 hours, as salticids are most responsive in the morning (Zurek and Nelson 2012b).

Before testing, salticids were removed from their jars and placed inside a cylinder that was open at one end, with holes drilled in the opposite, closed, end. Another cylinder, capped with foam where a spider was placed, was sized such that when it was plunged into the first cylinder, the spider was harmlessly restrained and the cephalothorax could be accessed through the holes. Once in position, the spider was fixed to a TPC® disposable micro-applicator by applying beeswax to the top of the cephalothorax. The micro-applicator with the spider attached was then suspended within the testing apparatus by a crocodile clip. The spider was given a 17 mm crosshair-marked polystyrene ball (weight 150 mg) to hold. This weight is easily held by sub adult and adult female *T. planiceps* (mean spider weight 53.26 (± 3.39 SEM) mg, n = 23; Melrose et al. In Press) for several hours without evidence of fatigue (see Zurek et al. 2010). Ten mm underneath the ball was a small ‘cup’ which caught the ball if the spider attempted to jump and dropped the

ball (Fig. 1). The ball was cleaned with 70% ethanol after each spider was tested to remove any chemicals deposited by previous individuals.

Once attached to the apparatus, the spider was equidistant (at 150 mm) from both monitors (Fig. 1). The salticid was given 20 min to settle from handling stress before being presented with a stimulus movie. Tests were conducted when salticids were hungry, having been without food for 6-8 days, and when they were sated, having eaten the previous day. The experiment consisted of a full-factorial design comprising stimulus type (low or high contrast circle), background clutter level (low or high) and hunger (hungry or sated) for each experimental unit (spider). Test sessions were blocked, such that each spider was subject to one stimulus type across two levels of clutter, when sated and when hungry. Overall, each spider was tested four times (2 clutter levels x 2 hunger levels), with presentation order randomised.

All tests were filmed with a Logitech® webcam to score responses. The orienting response of the salticid to a visual stimulus causes the polystyrene ball it is holding to swivel in the opposite direction to the stimulus (Zurek and Nelson 2012a). We recorded: 0 *no movement*; 1 *general activity*, such as walking on the ball, controlling for the possibility that any observed response decrement was not simply a freezing response or fatigue; 2 *fast responses* towards the stimulus, but not at optomotor speed; 3 *optomotor responses*, exceedingly fast whole-body swivels (c. 700^{o}/s) whereby the spiders (attempt to) turn towards the stimulus. Optomotor responses are highly characteristic of salticids and are unmistakeable (i.e. easy to distinguish from a 'fast' response).

All analyses were conducted in R v.3.3.1 (R Core Team 2016) using a proportional odds model that predicted the probability of a spider falling into a specific response category across the 80 trials. Data were analysed with a cumulative link mixed-effect model, assuming a logit link function, as the data were categorical. Individual differences between spiders were accounted for by including random effects into the model, assuming different intercepts and trial slopes for each spider. Model selection was used to determine an appropriate fixed-effects structure (containing first term and second order interactions). Potential models were compared and ranked through the 'AICcmodavg' package within R that selects the best model based on Akaike's Information Citerion (AIC) (Claeskens and Hjort 2008).

For visualisation, data were fitted as an exponential function $f(t) = \alpha e^{\lambda t}$ over 80 trials in MatLab© v.2015a (see Supp. Table 1 for best fit analyses). Here, λ is the decay rate, α is the initial quantity of the response, and *t* is the current trial. For this, the *no movement* category (category 0) was omitted and the *fast response* and *very fast response* categories (2 and 3) were merged.

Consequently, the exponential function of *activity* (response category 1) and *interest* (response categories 2 and 3) toward the stimulus were plotted in order to disambiguate any decrement arising from general fatigue.

Results

The analysis showed the probability of a spider movement falling into a certain response category over 80 trials (i.e., determining a slope for the vigilance decrement). Once ranked, the set of models were restricted to pairwise interactions only, based on the nature of the data. Thus, only the table for models with a maximum of 2-way interactions is shown. Overall, the best model showed significant effects of trial, hunger, and clutter level (Table 2) and all conditions elicited a response decrement.

Overall, activity levels were similar in all conditions (Figs. 2, 3), remained relatively flat across all 80 trials, and had similar variance around the mean (Fig. 3). Visually, activity levels increased slightly among sated spiders with a light stimulus at low clutter level and reduced slightly in saturated spiders for high contrast stimuli at the high clutter level; Figs. 2, 3). However, there was no statistical evidence of a change in general activity in any condition, so further discussion is omitted from the results. In contrast, while more variable than activity levels (Fig. 3), interest levels decreased markedly to near zero in all conditions, with the decay being steeper with the light stimulus, irrespective of hunger or clutter level (Fig. 2, raw data in Supp. Fig. 2). Specifically, the high contrast stimulus showed lower baseline responses (c. 43%) compared to the low contrast circle at the low clutter level (c. 69%), but the high contrast circle elicited a more gradual response decrement (mean decay rate = -0.026) compared with the low contrast circle (mean decay rate = -0.055). The decay rates (Figs. 2, 3) for the low contrast circle at the low clutter level when hungry (-0.061) and when sated (-0.036) differed, with the decrement being steeper in hungry spiders, especially in high clutter conditions. In contrast, the decay rates for the high contrast circle, irrespective of hunger level, were very similar (-0.025 and -0.021 when hungry and sated, respectively) across clutter levels (Figs. 2, 3).

Discussion

We tested the effect of task difficulty on vigilance decrement in salticids while considering the motivation (hunger) level of the test subject. There was a significant difference in vigilance decrement with both clutter and hunger levels. Hunger effects appeared to be less pronounced than stimulus contrast, with sated and hungry spiders responding fairly similarly in each of the low

contrast and high contrast stimulus conditions, suggesting that motivation is not as critical for the rate of the decrement as perceptual difficulty. This result is similar to that found in humans, which suggests that the decrement is not influenced as much by motivation as by challenge (Esterman et al. 2014). In people, motivation (typically a reward) tends to more strongly influence the overall detection rate, not the decline in detections over time (See et al. 1995), but our results show no clear pattern in which overall detection was affected by hunger. Essentially, we found that the impact of hunger and clutter level on decay rate was inconsistent and weak, in comparison to stimulus salience where the impact was more consistent, as also reported in humans (Esterman et al. 2014; See et al. 1995). We found no evidence of fatigue (reduction in general activity) in any condition, so we can discount motor fatigue as a factor in any observed decrement in response. Additionally, the decrement observed in *T. planiceps* was unlikely to be due to habituation. Full cessation of responses was not observed, and the slope of responses altered with difficulty, suggesting some level of processing. Additionally, a key pre-requisite for habituation is that, when given a dishabituating stimulus, the animal regains normal response levels (Thompson and Spencer 1966), yet this does not happen in *T. planiceps* (Melrose et al. In Press).

If the response decrement observed in invertebrates is comparable to the human literature on underload or understimulation (Pattyn et al. 2008), there should be a steeper decrement in tasks that are less demanding. Based on this theory, we would predict a steeper decrement to the easiest task of high stimulus contrast and low clutter. Alternatively, if the response decrement observed is comparable to the overload or overstimulation theory found in human literature (Helton and Warm 2008), we would predict a steeper decrement in response to the hardest task. We found that spiders exhibited a steeper decrement in the harder task which aligns with overstimulation, or the resource depletion theory (Helton and Warm 2008). Studies in humans (Grier et al. 2003; Helton et al. 2005; Helton and Warm 2008) and animals (Dukas and Clark 1995; Beauchamp and Ruxton 2012) have established that the central nervous system cannot sustain vigilance for an extended period of time (Nuechterlein et al. 1983; Warm 1984; Parasuraman and Mouloua 1987). Helton and Warm (2008) found that detection probability in humans was poorer for low salience signals compared to high salience signals and the vigilance decrement was steeper for the former. In *T. planiceps,* baseline responses to the high contrast stimulus were lower than in the difficult, low stimulus salience, condition, but revealed a shallower decrement compared with the low contrast stimulus, in which the spiders were initially more responsive, but responses decayed faster. The high baseline responses to the low contrast stimulus may be due to the spiders making more attempts to identify the stimulus. Despite the high spatial acuity of the AL

eyes (Zurek et al. 2010), when the circle was harder to see (low salience), the clutter obscuring it would have made it more difficult to disambiguate than when the circle was easier to see (high salience). This may also explain the larger variation in the data with the low contrast circle than with the high contrast circle. Insects, such as *Drosophila* (Poggio and Reichardt 1976; Heisenberg and Wolf 1984; van Swinderen and Greenspan 2003; Sareen et al. 2011) and praying mantises (Rossel 1980), respond selectively to salient visual stimuli, and this is likely true of spiders. Previous work has shown that about 40% contrast is an ideal level to elicit high rates of orientation responses in salticids (Zurek and Nelson 2012a). In the high salience condition, *T. planiceps* possibly determined quickly that the stimulus was not biologically relevant, explaining the low baseline responsiveness. Responses progressed differently over time, with the vigilance decrement to the low salience stimulus being steeper than that of the high salience stimulus. It is possible that sustaining attention to difficult stimuli (low salience) over about ten trials exhausted the replenishable cognitive resources required, as suggested for humans (Helton and Warm 2008).

Limited attention lowers the probability of detecting cryptic prey, and animals may be less likely to notice an approaching predator while engaged in an attentionally demanding task (Milinski 1990; Krause and Godin 1996; Dukas 2002). A larger attentional capacity should enable higher detection and more refined perception, but requires more neuronal tissue and concomitant metabolic cost dedicated to visual detection and information processing (Dukas 2002, 2004). Across all conditions, we can conclude that *Trite planiceps* individuals were initially selectively attentive to the low salient stimulus, but as task difficulty increased and thus became more cognitively demanding, their responses declined faster. These findings support the hypothesis that task difficulty affects the response decrement in *T. planiceps*, suggesting some level of higher-order processing in the vigilance decrement of spiders. Overall, the overstimulation theory seems a more reasonable hypothesis to explain the observed vigilance decrement in salticids, and, given their minute brains, this may not be entirely surprising. With our vastly larger brains, the human literature assumes this process to be centrally-mediated or 'top-down', yet from this study, we cannot conclude that the same is true of spiders, despite the similarity of the slope of the decrement between salticids and humans (Melrose et al. In Press). In honeybees, which are often used for studies on learning, attention and stimulus generalisation, visual attention-like processes begin in the optic lobes in the sensory periphery (Paulk et al. 2014). If this is true of spiders, given that our data suggest overstimulation of attentional processes, top down attention may not be required to explain the vigilance decrement observed in more complex mammalian systems, and

suggest that alternative interpretations of data from these more complex systems should be considered in future work.

Compliance with Ethical Standards

The authors declare that they have no conflict of interest and all applicable international, national, and institutional guidelines for the care and use of animals were followed.

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Table 1. Characteristics of clutter levels and stimuli used in experiments on *Trite planiceps*. For clutter, the level percentage and for stimuli, the contrast, luminance, brightness and RGB values were measured within Photoshop®. Weber contrast measured as $I_{stimulus} - I_{background}/I_{background}$.

Clutter level (%)	Luminance (cd/m2)	Brightness (%)	RGB	Weber contrast
20	92	91	232, 232, 232	-0.061
40	85	83	211, 211, 211	-0.133
Stimulus contrast (%)	**Luminance (cd/m2)**	**Brightness (%)**	**RGB**	**Weber contrast**
10	94	94	239, 239, 239	-0.041
30	85	84	213, 213, 213	-0.133

Table 2. Model-selection results for evaluating clutter levels and stimulus salience on responses to repetitive visual stimuli in *Trite planiceps*. Effects included are the fixed effects (T = trial, D = stimulus type, H = hunger level, C = clutter) and their pairwise interactions*. K is the number of estimated parameters for each model, AICc is Akaike's Information Criterion, Δ AICc is the appropriate delta AIC component. AICcWt is the Akaike weights. N=19. These are the most important models as a subset of the full set of possible models and their relative contributions.

Effects included	Model	K	AICc	Δ AICc	AICcW
All terms excluding stimulus effects	(T+H+C)*	12	12146.82	0.00	0.77
All terms	(T+D+H+C)*	16	12149.20	2.38	0
Trial, clutter	(T+C)*	9	12185.35	38.54	0
All terms excluding hunger effects	(T+D+C)*	13	12186.59	39.78	0
Trial, hunger	(T+H)*	9	12213.12	66.30	0
All terms excluding clutter effects	(T+D+H)*	12	12215.07	68.26	0
Trial	T	7	12215.29	68.48	0
Trial, stimulus	(T+D)*	9	12216.18	69.36	0

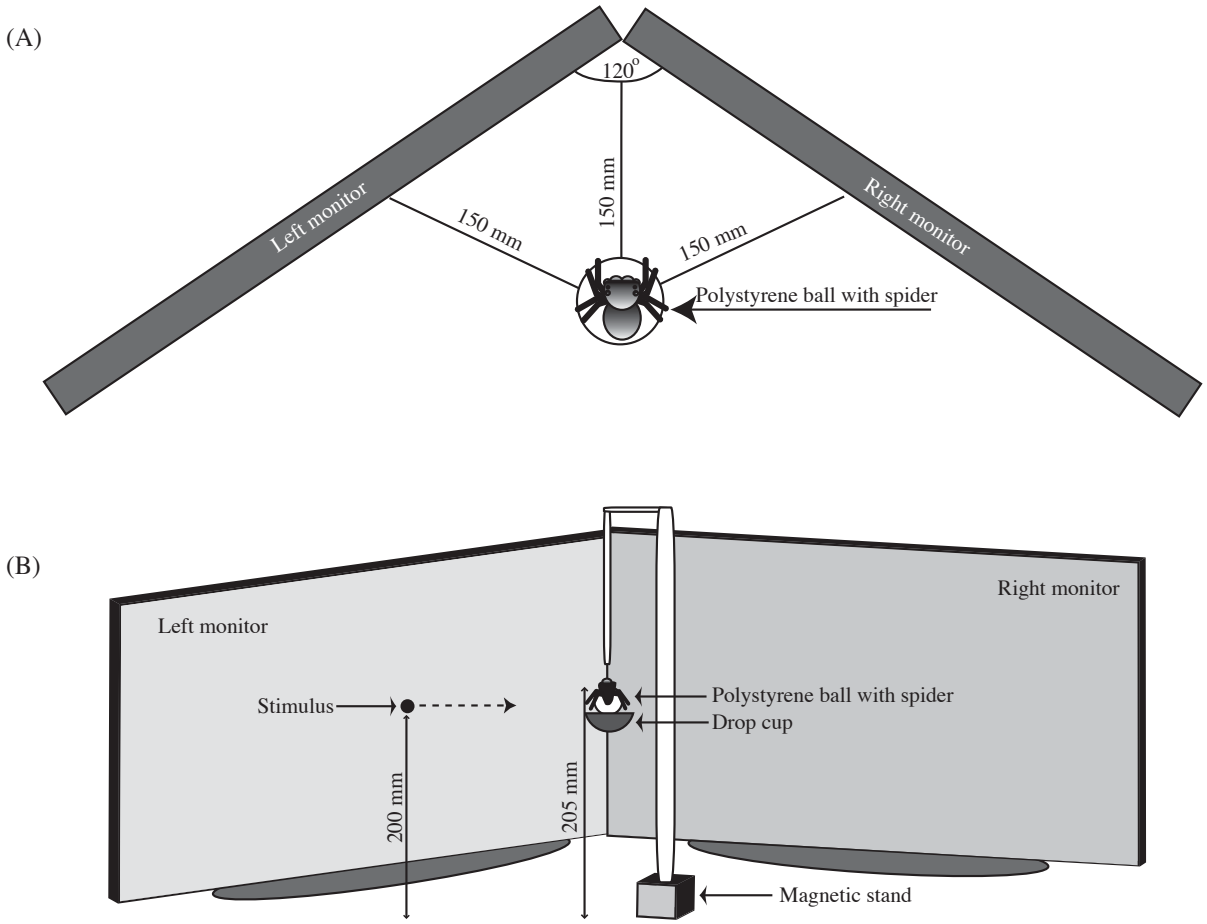

Fig. 1 Apparatus used for testing *Trite planiceps*. (**a**) Aerial view of the salticid holding the polystyrene ball. (**b**) Frontal view demonstrating the position of the rig holding the salticid. The drop cup catches any dropped balls which are close enough for the salticid to retrieve. A small platform supports the drop cup (not shown).

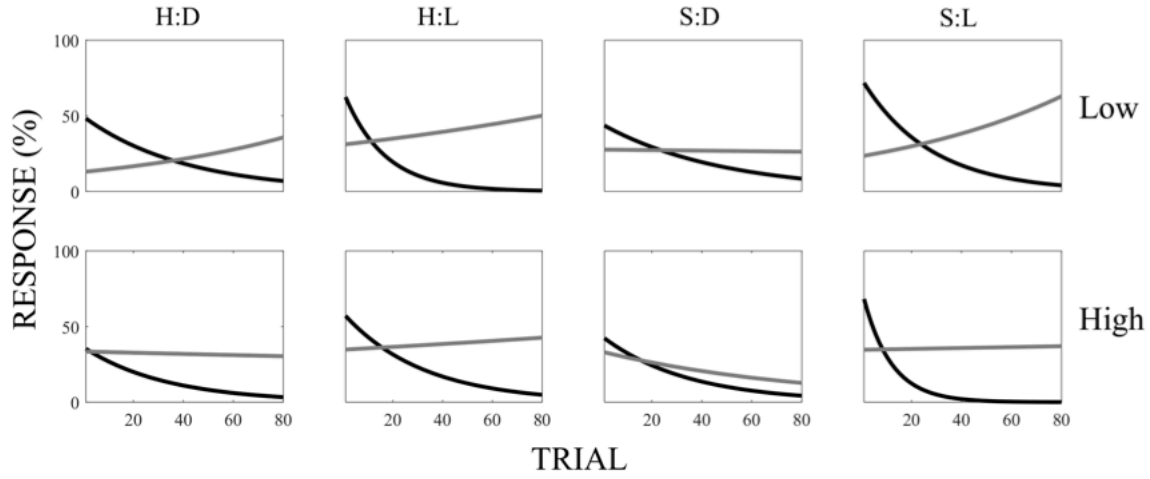

Fig. 2 Exponential regression of the responses in *Trite planiceps* over 80 trials. Hungry and sated spiders were shown repeated stimuli of a 40-pixel dark, or high contrast circle or a light, or low contrast circle, against two levels of clutter (low and high). Grey lines depict general movement; black lines represent distinct responses (combining optomotor and fast responses) toward the stimulus. Data are based on those used in Fig. 3.

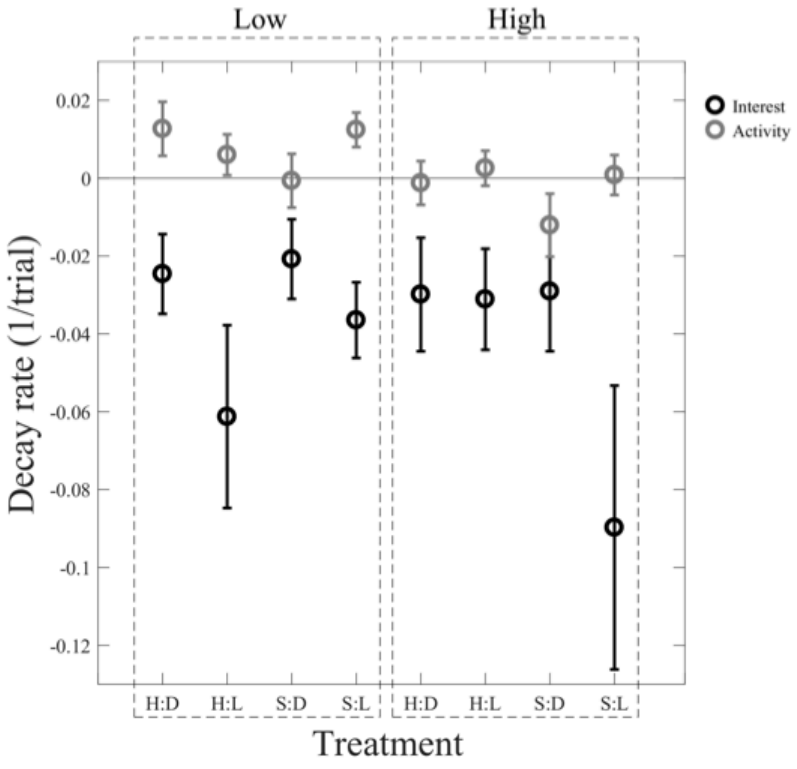

Fig. 3 Mean (± 95% confidence intervals) for the response decay rate in *Trite planiceps* fitted as an exponential function over 80 trials. Spiders, when 7 days hungry and sated (on X-axis), were shown repeated stimuli of a 40-pixel high or low contrast circle (on x-axis) against low (left panel) and high (right panel) levels of clutter. Grey depicts general movement, while black represents distinct responses (combining optomotor and fast responses) toward the stimulus.

Supplementary Material

Table S1 Root Mean Squared Error (RMSE) of the tested statistical models; lower RMSE values indicate a better fit. The regressions were estimated from 80 trials performed on *Trite planiceps* individuals when seven days hungry and sated ('H' and 'S', respectively). Stimuli consisted of a dark or light contrast circle ('D' and 'L', respectively) against 'low' and 'high' levels of clutter. RMSE values are presented for distinct responses and general movement ('DR' and 'GM', respectively).Bold numbers represent the best fit for each specific case.

		Hungry, Dark				Hungry, Light				Sated, Dark				Sated, Light			
		Low		High		Low		High		Low		High		Low		High	
	Function	*DR*	*GM*	*DR*	*GM*	*DR*	*GM*	*DR*	*GM*	*DR*	*GM*	*DR*	*GM*	*DR*	*GM*	*DR*	*GM*
RMSE	Exponential $f(x) = ae^{bx}$	**12.297**	11.584	**10.303**	**13.749**	**9.7765**	16.374	**13.468**	13.054	13,525	**13.760**	15.967	12.872	**11.550**	22.327	**10.243**	**13.805**
	Polynomial $f(x) = ax + b$	15.130	11.480	12.892	14.026	15.369	16.179	17.614	13.502	15,592	14.531	16.315	**12.719**	15.645	12.451	15.120	14.365
	Power $f(x) = ax^b$	12.417	**11.421**	10.635	13.985	9.9377	**15.773**	13.877	**12.862**	**13,389**	14.458	**14.264**	13.793	12.547	11.805	10.527	14.179
	Rational $f(x) = a/(x + b)$	12.910	13.430	10.902	14.022	10.491	17.134	14.510	13.751	14,201	14.533	14.679	12.983	11.591	18.010	10.693	14.384
	Sinusoid $f(x) = a\sin(bx + c)$	15.228	11.540	12.976	14.117	15.469	16.282	17.728	12.500	15,693	14.269	16.421	12.752	15.747	**11.729**	15.218	14.174

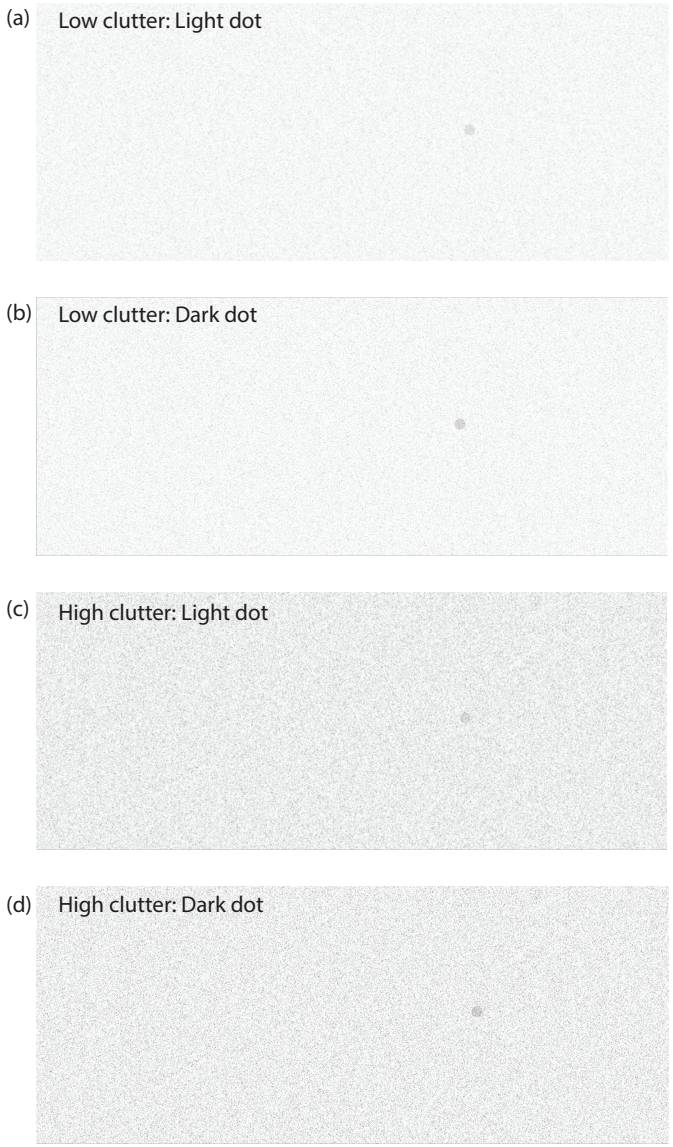

Fig. 1 Stimuli used in experiments with *Trite planiceps* spiders. (a) shows the low contrast stimulus (10%) against low (20%) clutter, (b) high contrast stimulus (30%) against low (40%) clutter, (c) low contrast stimulus against high clutter, and (d) shows the high contrast stimulus against high clutter.

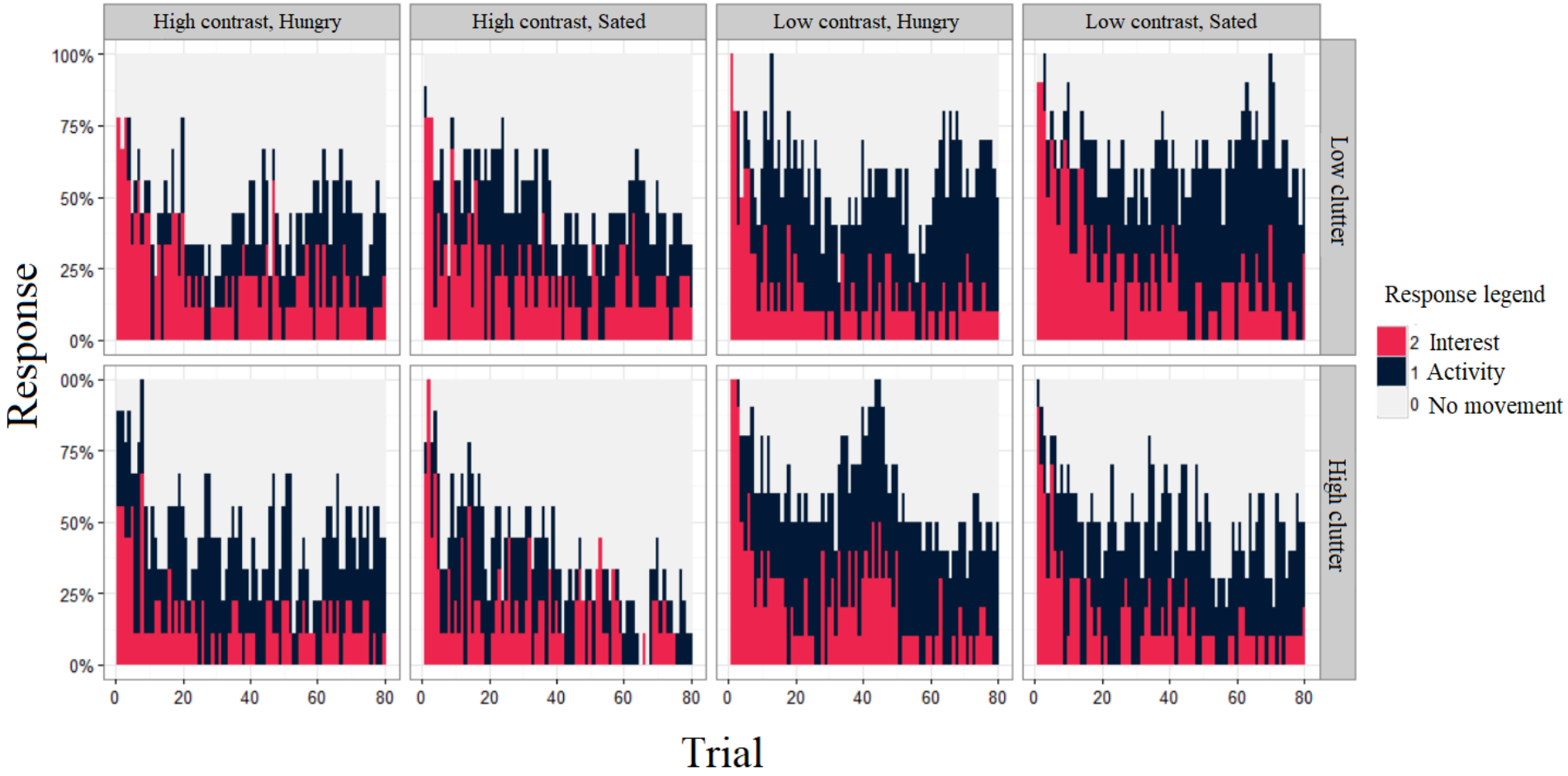

Fig. 2 Raw data depicting responses of *Trite planiceps* spiders to visual stimuli. Hungry and sated spiders were shown repeated stimuli (80 trials) of a 40-pixel high contrast circle or a low contrast circle, against two levels of clutter (low and high). Behaviours were recorded as: no movement (0); general activity, such as walking on the ball (1), and interest, such as attempts to orient toward the stimulus (2).